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Temporal coherence in visual rotation

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Abstract

The brain can predict and estimate motion based on visual translation. This paper addresses whether the visual system also has a specialized mechanism of temporal coherence for rotational motion. To do this, we measured the perceived mislocation of a rotating dot at the time of its luminance transition. Results show that subjects mislocate the dot consistently with its circular motion rather than with translational temporal coherence. We propose a model to explain these results based on a combination of an error in a location-estimation task and on the brain assuming rotational motions.

Keywords: Motion; Rotation; Temporal coherence; Localization; Flash-lag

1. Introduction

The visual perception of motion is one of the most important functions of the brain. Its visual system begins to perform this task by estimating motion parameters in small regions of the image (Grzywacz, Harris, & Amthor, 1994). These local estimations tend to be noisy (Shadlen & Newsome, 1998) and are often ambiguous (Movshon, Adelson, Gizzi, & Newsome, 1985). To solve these problems, the visual system combines its local estimates of velocity across space (Watamaniuk & Sekuler, 1992) and time (McKee & Welch, 1985). For instance, the brain disambiguates, predicts, and estimates motion through temporal coherence, that is, by assuming that objects move in consistent trajectories rather than abruptly changing their direction (Burgi, Yuille, & Grzwacz, 2000; Ramachandran & Anstis, 1983; Watamaniuk, McKee, & Grzywacz, 1995). Other motion phenomena involving temporal coherence include the improvement of velocity estimation over time (McKee, Silverman, & Nakayama, 1986), blur removal (Burr, Ross, & Morrone, 1986; Watamaniuk, 1992), detection of motion-outliers (Watamaniuk et al., 1995), and motion occlusion (Watamaniuk & McKee, 1995). These motion phenomena have challenged motion-perception models based exclusively on single, large-local motion detectors as in the motion-energy and elaborated-Reichardt models (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). This point is emphasized by the human performance in the detection of long trajectories not being achieved by the sum of their local parts (Verghese, Watamaniuk, McKee, & Grzywacz, 1999). This suggests that the improvement of the detectability over long durations (McKee & Welch, 1985; Snowden & Braddick, 1989) could well be due to high-level neural mechanisms that integrate local motion signals (Watamaniuk & Sekuler, 1992). Recently, the study of the temporal integration of motion was extended to optic-flow stimuli (Burr & Santoro, 2001), which are the motion patterns that occur on the retina when one is navigating through the environment (Gibson, 1950; Koenderink & van Doorn, 1976). The integration times for coherent translation, rotation, and divergence are of the order of seconds, while those for contrast sensitivity are at least 10 times faster. The analysis of complex coherent motion probably takes place in cells sensitive to complex flow patterns that have been reported in the middle temporal and the dorsal portion of the middle superior temporal areas of the cortex (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Tanaka & Saito, 1989). Such cells are consistent with psychophysical data demonstrating that there are high-level mechanisms that encode complex motion by combining signals from

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more elementary detectors tuned to different directions of motion (Morrone, Burr, & Vaina, 1995).

In this paper, we explore whether the human visual system also uses the parameters of rotation to predict and estimate motion, that is, whether the brain has a rotational temporal-coherence mechanism. We do so by exploiting an effect related to the mislocation of moving objects at the moment of their disappearance, such as reported by Mateeff et al. (1991). These authors found a systematic location error towards where motion was going for translational trajectories. Here we test whether if one produces such an effect by using rotation instead of translation, then the mislocation is consistent with the circular trajectory rather than with the instantaneous linear velocity at the time of disappearance or of a luminance change.

2. Methods

2.1. Stimuli

In preliminary experiments, we observed that if the luminance of a moving dot was suddenly changed without stopping the motion, subjects mislocated the position where the transition occurred. This is an interesting effect, which can be used to explore the mislocation of moving dots without using any external temporal reference, such as a brief tone or a flash. Hence, we replaced the disappearance of the test dot used by Mateeff et al., by an abrupt luminance transition in the stimulus during its continuous motion. The stimulus was a 30-dot annulus revolving with a fixed angular velocity around a center for 1024 ms. The dots appeared on a high-resolution CRT monitor set with a background luminance of 39 $\mathrm{cd\,m^{-2}}$. One of the dots (white) had a luminance of 58.5 $\mathrm{cd\,m^{-2}}$ and was considered the test dot. The other dots (black dots) had a luminance of 19.5 $\mathrm{cd\,m^{-2}}$ and were presented to the observer to strengthen the signal of the rotation. The radius of the annulus was 1.82° viewed from a distance of 0.5 m and the size of the dot was 11′. The luminance transition was presented always at the middle of the presentation (512 ms), and consisted in abruptly changing the luminance of the white test dot to that of the black dots. The angle of luminance transition (ϕ) was defined by two imaginary line sections. These sections left the center of the circle, one going towards the position of the luminance transition and the other towards the top of the circle. Positions to the left and to the right of the center defined negative ($\phi < 0$) and positive ($\phi > 0$) angles, respectively.

2.2. Procedure

The procedure was as follows: after 48 ms of the luminance transition of the test, a static line (horizontal or vertical) was presented as a spatial reference for 64 ms. The presentation of this line was delayed to avoid its use as a temporal reference. [1] Although such a short delay could affect the absolute values of the mislocation (Krekelberg & Lappe, 1999), the delay could not mask the effect that we wanted to show, that is, that the mislocation was consistent with rotational temporal coherence. For the case of the Y dimension, subjects had to report, by pressing a key of the mouse, whether the white test dot was above or below a horizontal line when the luminance transition occurred. Moreover, For the case of the X dimension they had to report whether the white test dot was to the right or to the left of vertical line when the luminance transition occurred. The fixation mark was 2.32° away from the center of the annulus, with the same angle as the luminance transition for each block of trials. Although the spatial reference was presented a time after the luminance transition occurred, subjects could perform the task without any inconvenience.

A 2AFC paradigm using the method of constant stimuli was used to obtain the subjects' psychometric functions. Perceptual location of the luminance transition was calculated by fitting a cumulative Gaussian curve to these functions. To obtain them, a set of six stimuli was used in each of two blocks of trials. Each stimulus was used a total of 20 times per block.

2.3. Subjects

Three subjects took part in this experiment, one of the authors and two others naïve as to the purpose of the study. All subjects had normal or corrected-to-normal vision, and were experienced in visual-motion experiments.

3. Results

3.1. Mislocation as a function of the angle of luminance transition

We measured the perceptual location of a moving white dot (test) at the moment of its luminance transition with respect to a static line. Before the luminance transition, this dot was undergoing a clockwise rotation with an angular velocity of 3.75 $\mathrm{rad\,s^{-1}}$. The test was one of 30 dots arranged in an annulus concentric and with the same radius as the circular motion (Fig. 1A). All the dots, except for the test, were black. The white dot was set to change its luminance in one of six points on the upper portion of the annulus. One of these points cor-

[1] A possible dependence of the magnitude of the mislocation on delay has been tested. We measured the mislocation for another delay, 96 ms, and obtained the same result as that for 48 ms.

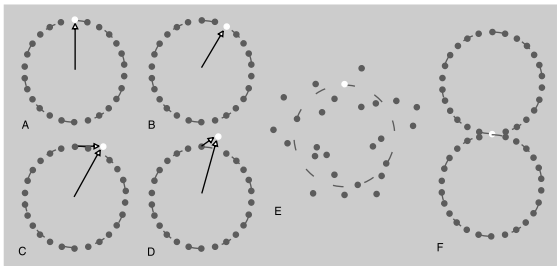

Fig. 1. Schematic of visual stimuli. Panel A shows an example of the stimulus, in which the test dot (white) "disappears" (turns black) at the top of the circle ($\phi = 0$). In other words, the last frame of the test dot occurs at this point. Panel B shows schematically the subject's percept of the dot's location of the dot. The test dot seems to disappear ahead of its actual position but consistently with its circular trajectory (with $\phi > 0$). In other words, the dot seems to disappear to the right and below its actual disappearance location. Panel C shows the prediction of the hypothesis that the mislocation depends on the instantaneous local linear velocity at the time of the disappearance. In this case, the expected spatial shift occurs only in the X dimension, because the vertical component of velocity is zero. The hypothesis that the mislocation depends on a translational version of temporal coherence makes an even worse prediction (Panel D). Because instantaneous translations before the time of disappearance had an upward component, the prediction is that the test appears above the circle. Panel E shows an example of the stimulus with positional jitter. Panel F shows the ambiguous "Figure-8" stimulus. The upper and lower annuli rotate in counterclockwise and clockwise directions, respectively. Only the lower annulus contains the test (white dot). The fixation point is located 0.6° to the right of the intersection of the annuli.

responded to the top of the circle ($\phi = 0$). Subjects mislocated this dot according to rotational temporal coherence (Fig. 1B) but not according to either the instantaneous velocity (Fig. 1C) or a translational temporal-coherence assumption (Fig. 1D). We measured both the X (horizontal) and Y (vertical) perceptual locations of the dot at the time of the luminance transition as a function of the angle of luminance transition.

Fig. 2 shows the perceptual location of the test as a function of the actual angle of the luminance transition. Results in the Y dimension (top-right plots in both panels) show that for negative angles, the test dot is perceived above its actual position (dashed line) when the luminance changes. In contrast, for zero and positive angles, the perceptual transition takes place below its actual position. These mislocations cause the data curve to be displaced to the left of the actual-positions curve (two-sided t-test, five degrees of freedom (DF), $p < 0.001$ for JB and $p < 0.0004$ for VA). [2] Furthermore, if one shifts the actual-positions curve leftward (by 0.13 rad for JB and 0.14 rad for VA), then the resulting curves fit the data well (solid line). This fit shows that subjects see the test dot disappear ahead of its actual position but in a point on its circular trajectory. As a result, the magnitude of the mislocation is not proportional to the instantaneous vertical component of velocity. For instance, for $\phi = 0$, despite the vertical component of velocity being zero, the dot is seen to disappear below its actual position (two-sided t-test, five DF, $p < 0.0002$ for JB and $p < 0.00002$ for VA). Results obtained in the X dimension (bottom-left plots in both panels of Fig. 2) are also consistent with a mislocation based on a rotational assumption. They show that the test is perceived to disappear to the right of its actual position, resulting in a downward shift of the data curve (two-sided t-test, five DF, $p < 2 \times 10^{-5}$ for JB and $p < 6 \times 10^{-8}$ for VA). And again, the data can be fitted well by shifting the actual positions curve downward (by 0.13 rad for JB and 0.14 rad for VA). Importantly, these fits were obtained for both the Y and X dimensions independently, showing surprisingly the same phase shift. The top-left plots in both panels of Fig. 2 show a combination of Y and X panels. In these new panels, the perceptual location of the test dot, at the time of the luminance transition, in Y dimension is plotted as a function of the perceptual location in X dimension. These plots show how the data produce a rotated circle. Therefore, subjects see the test dot change its luminance ahead of its actual position in a point belonging to the circular trajectory.

3.2. Controlling for form cues

Is the circular-trajectory mislocation due to the brain assuming the motion to be a rotation? An alternative is that the brain is using the form signal in the stimulus to locate the dot. In this case, a circular form is defined by the black dots and the brain could place the dot in the circle, independently of the rotational motion. We performed two experiments to control for these alternatives.

In our first control of the form cue alternative, we propose to break the circular shape of the stimulus by adding a positional jitter to the black dots (Fig. 1E). In this case, the stimulus is not providing the form cue to the subject. Therefore, the mislocation in the Y dimension should not occur. The positional jitter was achieved by giving each black dot a trajectory radius that could randomly vary in a range defined by a percentage of the radius of the white dot. In other words, each black dot could have any radius between $R(1-f)$ and $R(1+f)$, where R is the radius of the white dot and $0 \geqslant f \geqslant 0.5$. The procedures and the values of R, dot size, and luminance were the same as in the previous experiments. This experiment was carried out with two naïve subjects. From it, we measured the magnitude of the mislocation in the Y dimension as a function of the percentage of positional jitter in the stimulus, for the "$\phi = 0$" luminance transition. Fig. 3 shows the magnitude of the

[2] Statistical t-tests were carried out separately for the X and Y dimensions. One two-sided t-test was performed for the X dimension and another two-sided t-test was performed for the Y dimension.

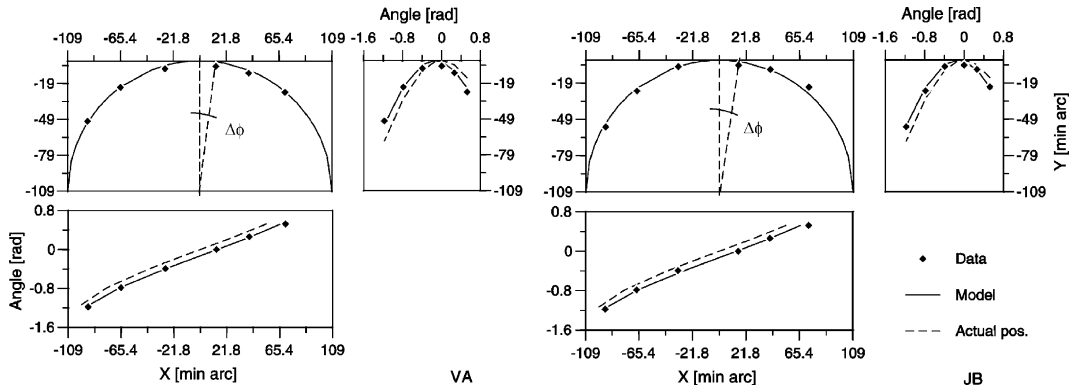

Fig. 2. Results of the main experiment. The left panel corresponds to Subject VA and the right panel B to Subject JB. In each panel, the perceptual location of disappearance of the test dot as a function of the angle of disappearance for the Y dimension appears on the top-right plot. The same plot for the X dimension appears on the bottom left. Finally, the perceptual location of disappearance of the test dot in the X–Y plane appears in the top-left plot. In the X–Y plot, each perceptual location obtained in Y is plotted as a function of that obtained in X for the same angle. Both the top-right and bottom-left plots show the data as solid diamonds, phase-shifted sinusoidal functions as solid lines, and the actual position of disappearance as dashed lines. In the X–Y panel, a circumference arc with the same radius as the annulus and concentric with it appears as a solid line. The $\Delta\phi$ angle shows the measured angular mislocation of the test.

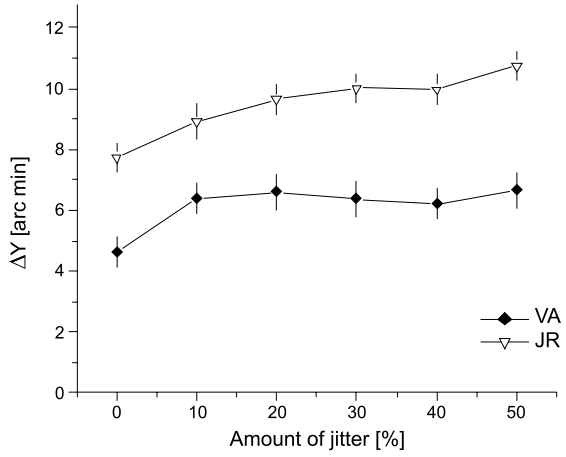

Fig. 3. Magnitude of the vertical mislocation as a function of the percentage of spatial jitter added to the stimulus. Results for two observers show that even with a jitter of 50%, the effect of mislocation persists, which indicates that the brain is not using the form signal to locate the white dot.

mislocation as a function of jitter, expressed as a percentage of the white-dot radius. The plots for both subjects show that the mislocation remains constant with the variation of the amount of jitter. This means that this parameter has no influence on the mislocation effect. This result suggests that the brain is not using the stimulus-form information to locate the white dot.

In a second control of the form-cue alternative, we modified the original experiment to produce an ambiguous stimulus. We added to the original annulus another one with the same number of dots, all of them black, and the same radius (Fig. 1F). The new annulus rotated counterclockwise and its center was at a distance of two radii above that of the original annulus, so that the top dot of the lower circle was shared by the top annulus. The percept of this stimulus alternated over time between two independent circles and a single shape in the form of an 8. This perceptual bi-stability occurred both when all dots were black and when the stimulus contained the white test dot. We reasoned that the rotational motion and circular-path hypotheses would predict different results for the perceptual location of luminance transition of the test dot for $\phi = 0$ (the shared point). According to the first hypothesis, the results would not be affected by the ambiguity, that is, this location would always be in the lower annulus. However, according to the second hypothesis, the probability that the dot is seen on the upper annulus is exactly the same as on the lower annulus. The solid line in Fig. 4 shows the psychometric functions, indicating the proportion of times that the subject sees the dot above a static reference line [3] as a function of the height of this line. For the Figure-8 paradigm, when the line is exactly between the two annuli ($y = 0$), this proportion is much smaller than 0.5. That this value is small shows that subjects tend to see the dot on the lower annulus. Therefore, the data in Fig. 4 is again consistent with the rotational-motion hypothesis but not with the circular-path hypothesis.

3.3. Mislocation as a function of velocity

Because the mislocation is consistent with rotational temporal coherence, we hypothesized that this misloca-

[3] This does not mean, however, that the upper motion did not affect the test dot. Fig. 4 shows that such an effect exists. In this figure, the Figure-8 psychometric functions are compared with those obtained for the same angle in the previous experiments. The results show that the Figure-8 psychometric curves are shifted up from the single-annulus curves, which means that the perceived misalignment is smaller.

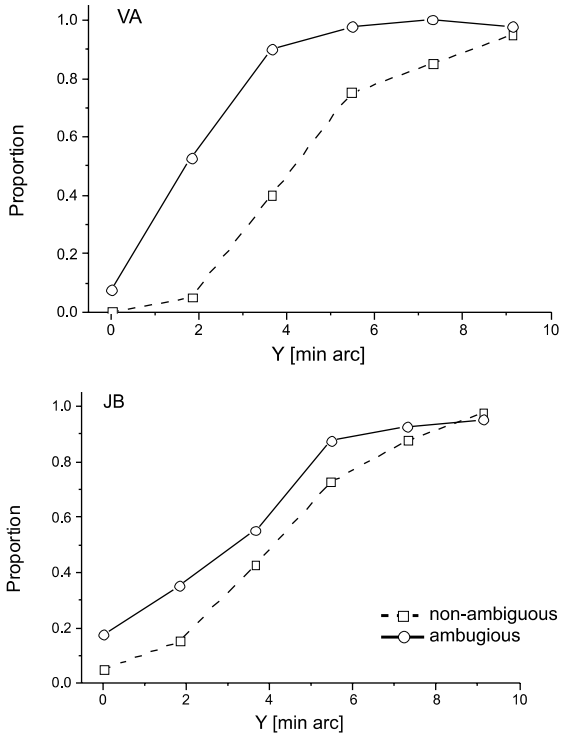

Fig. 4. Psychometric curves obtained with the Figure-8 (solid line) and single-annulus (dashed line) stimuli. These curves indicate the proportion of times that subjects see the position of luminance transition above a static reference line as a function of the height of this line (Y). For the Figure-8 stimulus, when the lime is exactly between the two annuli ($y = 0$), subjects tend to see the dot disappearing on the lower annulus, as indicated by the proportion being smaller that 0.5. However, this proportion is higher than that obtained with a single annulus for all line heights.

tion increases monotonically with angular velocity. To test this hypothesis, we measured the magnitude of the mislocation in the Y dimension as a function of velocity for a $\phi = 0$ luminance transition. Fig. 5 shows that the magnitude of the mislocation increases monotonically with velocity, consistently with our prediction. However, this magnitude seems not consistent with an angular mislocation proportional to angular velocity. In this case, the angular mislocation should be $\phi = \omega\Delta t$ and therefore, the mislocation in the Y dimension should follow the sublinear geometrical relation $\Delta Y = R(1 - \cos\omega\Delta t)$. Here, R is the radius of the annulus, ω is the angular velocity, and Δt is a constant period during which the mislocation would occur. To test this prediction, we performed a non-linear regression to find the parameter Δt that gives the best fit of this function to the data. This fit is represented by the dotted line in Fig. 5. We then plotted the data as a function of the prediction (not shown), and tested whether this plot can be represented by a straight line passing through the origin and with a slope of 1. Results showed, for both observers, that the probability that this line crossed the origin was less than 0.001 (two-sided t-test). Furthermore, the slopes obtained for Subjects VA and JB were 0.60 ± 0.12 and 0.72 ± 0.14, respectively, being statistically different from 1 (two-sided t-test; $p < 0.015$). Therefore, our data did not follow the prediction of linearity between angular offset and angular velocity. This was not consistent with previous results, which had shown such a linearity (Krekelberg & Lappe, 1999). Perhaps, this discrepancy was due to differences in the experimental setup. In particular, our study focused on the position of a moving dot at the time of its luminance transition, instead of the position of the dot relative to an external reference, as in the flash-lag experiments.

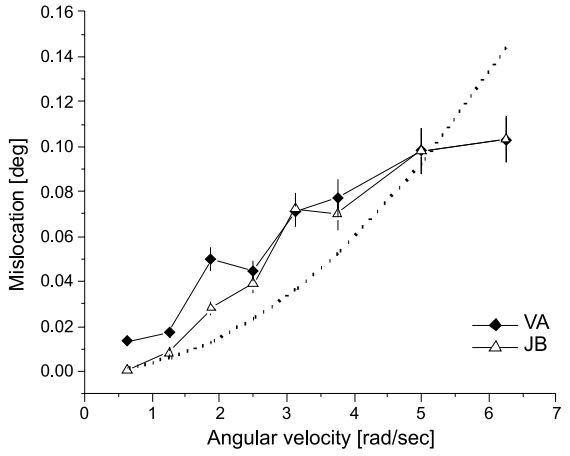

Fig. 5. Magnitude of the mislocation in the Y dimension as a function of angular velocity. This magnitude increases monotonically with the angular velocity for two observers, consistently with a rotational temporal-coherence model. However, the magnitude does not follow the prediction of linear dependence on angular velocity, showed in the figure by dotted line.

4. General discussion

The results presented here show that the location estimation of a moving dot at the time of its luminance transition can be systematically biased by its rotational motion. For example, when the luminance change occurs on the top of the circle, the dot is seen below its actual position. Moreover, the phase-space plots in Fig. 2 show that the mislocation is consistent with the circular motion. Neither the instantaneous velocity nor a translational temporal-coherence model can explain these results. Hence, the visual system appears to include rotational temporal coherence.

How can mislocation be explained? There is a great amount of literature analyzing phenomena related with mislocations of moving stimuli (for example: Baldo & Klein, 1995; Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000; Kirschfeld & Kammer, 1999; Krekelberg & Lappe, 1999, 2000; MacKay, 1958; Mateeff, Bohdanecky, Hohnsbein, Ehrenstein, & Yakimoff, 1991;

Mateeff et al., 1991; Mitrani & Dimitrov, 1982; Nijhawan, 1994, 1997, 2001; Rao, Eagleman, & Sejnowski, 2001; Whitney & Cavanagh, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000), and specially, on the flash-lag effect. This effect refers to the misalignment perceived when a static stimulus is briefly presented adjacent to a moving stimulus (for a review, see: Krekelberg & Lappe, 2001). Several models have been proposed to explain this effect (Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Nijhawan, 1994; Rao et al., 2001; Whitney et al., 2000). The model by Nijhawan would seem to be consistent with our results. According to this model, the brain could be extrapolating the position of the white dot to the "expected" location and thus, the luminance transition would be seen ahead from where it actually occurred. However, this model would not be parsimonious, since there is much evidence against motion-extrapolation models (for example, Whitney & Murakami, 1998). Alternatively, an explanation such as that by Rao et al. (2001) can also be consistent with our data. They proposed a model based on an optimal temporal smoothing. If one thinks that this smoothing delays the luminance transition, then the white dot could be seen for a while, after the luminance transition, over the circular trajectory. This explanation is also consistent with the delay being due to the estimate of positions being performed within a time window during which temporal averaging occurs (Krekelberg & Lappe, 2000).

Yet another alternative is that the mislocation is due to an error in a position-estimation task. To perform such a task, the brain would be "wise" to consider data from neurons whose receptive fields are roughly concentric with the position where the luminance transition occurs and also from neighbor neurons. Given these data, the visual system may perform this task optimally despite neural noise. However, if neural circuits are designed mostly for localization in stationary conditions, then these circuits may be optimized so that the responses of neighbor neurons around the central neurons are spatially symmetric. This assumption is incorrect following motions. Because cells have non-instantaneous impulse responses, motion induces an asymmetry in the response distribution across neighbors. Therefore, the brain would have to deal with this asymmetric distribution to estimate the location of the moving test. How may the brain do this? We propose a mechanism that fits the response distribution according to the following two assumptions: First it is assumed that the stimulus is moving with a constant speed. Second, the location estimation would be delayed to allow the cell's response to get its maximum. Using these assumptions, the location in the stimulus trajectory that fits the data best is tested. Because of noise and the asymmetry of the response distribution across cells, the fit would be systematically biased towards the direction of motion. We implemented this idea in a computer model and confirmed that under the mentioned assumptions, this bias occurs. This model has substantial differences from the models mentioned above. In our model, the spatial mislocation is due to an error in the location-estimation task. The error is due to the cells' temporal properties, which may not be specific to motion. In contrast, the other models explain the effect through motion-specific mechanisms such as, for example, optimal smoothing (Rao et al., 2001). This mechanism is such that the location-estimation task is mediated by a predictive process (Kalman filtering), which produces the mislocation.

One thing missing in these explanations for the mislocation is a reason for why the mislocation is consistent with the circular trajectory. Our hypothesis is that the brain assumes the motion to be a rotation. Thus, because of temporal coherence, the brain would try to estimate the dot position coherently with the past rotational motion. There are arguments that support our hypothesis. For example, it is known that the human visual system prefers to see an object move in a consistent direction rather than abruptly change its direction. Such a phenomenon may be possible also for rotational motion if an appropriate mechanism of temporal coherence is applied. There are many psychophysical studies suggesting that the brain has specialized mechanisms to analyze optic-flow components, including rotations (Barraza & Grzywacz, in press; Freeman & Harris, 1992; Morrone et al., 1995; Regan & Beberley, 1985). Furthermore, physiological studies show that there are cells in the middle superior temporal cortex specifically selective to such complex flow patterns (Duffy & Wurtz, 1991; Graziano et al., 1994; Tanaka & Saito, 1989). Finally, a recent paper has shown that the coherence thresholds for translational, rotational, and radial components of the optic flow improve with the stimulus duration for several seconds (Burr & Santoro, 2001). This suggests that there could be temporal-coherence mechanism for these complex motions.

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